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Antheraea castanea Jordan, 1910, the neglected "pseudomuga" silkmoth (Lepidoptera, Saturniidae)

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Abstract

This study reports the first complete life history of *Antheraea castanea* Jordan, 1910. Samples collected from the southeastern borders of Yunnan and Tibet were reared on specific species within the family Lauraceae, confirming that *A. castanea* is univoltine in captivity. The complete mitochondrial genome sequences of *A. castanea* and *Antheraea youngi* Watson, 1915, both belonging to the subgenus *Antheraeopsis* Wood-Mason, 1886, are provided. Genomic and morphological evidence demonstrates that *A. castanea* is the sister group to all other *Antheraeopsis* spp. This finding strongly supports the hypothesis that this subgenus originated in the southeastern regions of the Himalayas, making *A. castanea* a key taxon for understanding the evolutionary history of the genus *Antheraea* Hübner, 1819. Given its long-standing neglect in sericulture, we recommend increased attention to *A. castanea* in future studies—particularly to prevent misidentification with the muga silkmoth, *Antheraea assamensis* (Helfer, 1837), which shares similar habitats.

Key Words

Antheraeopsis, complete mitochondrial genome, India, Lauraceae, life history, morphology, muga, phylogeny, sericulture, Tibet, wild silkmoth, Yunnan, zoogeography

Introduction

The famous muga silkmoth, *Antheraea assamensis* (Helfer, 1837), is one of the most economically important species in Northeast India (e.g., Peigler 1993, 2020). The sericulture of this species in Assam was reported in early literature (e.g., Hugon 1837), and it remains a current hot topic in saturniid studies. As one of the three clades constituting the genus *Antheraea* Hübner, 1819 (Nässig 1991), the muga subgenus *Antheraeopsis* Wood-Mason, 1886, is restricted to subtropical and tropical Asia. Kitching et al. (2018) listed 12 currently accepted species. Based on their type localities, these include Sichuanese *Antheraea chengtuana* Watson, 1923; Taiwanese *Antheraea formosana* Sonan, 1937; Andamanese *Antheraea rudloffi* Brechlin, 2002; Sumatran *Antheraea brunnea* van Eecke, 1921; Bornean *Antheraea youngi* Watson, 1915; Javan *Antheraea rubiginea* Toxopeus, 1940; Palawan *Antheraea sahi* Nässig & Treadaway, 1998; and Philippine *Antheraea paniki* Nässig & Treadaway, 1998. However, *Antheraea inthanonensis* Paukstadt & Paukstadt, 2013, and *Antheraea tenasserimensis* Paukstadt & Paukstadt, 2013, from Thailand are very close to *A. assamensis* in terms of morphology and barcoding—we believe they are better treated as different subspecies or even synonyms.

Another species, originally collected in the Meghalayan Khasi Hills, was named *Antheraea castanea* Jordan, 1910, but it has not been discussed by Indian authors except for Gupta (2000). Naumann et al. (2008) confirmed that *Antheraea mezops* Bryk, 1944, which is typically from Burmese Kambaiti, is a junior synonym of *A. castanea*. All Chinese specimens in our hands were captured only in the rain-rich broadleaf forests at elevations of ca. 1200–2200 m in Mêdog, Tibet (Fig. 1B),

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Figure 1. Living adults of *Antheraea castanea*; dates indicate photography dates. **A.** ♂, Gaoligong Mountains, Baoshan, Yunnan, 2214 m, 22 June 2025 (the moth was photographed locally); **B.** ♀ No. 6, Mêdog County, Nyingchi, Tibet, 2182 m, 06 July 2025 (the moth was captured locally and sent to Kunming, Yunnan, for photography). Scale bars: 3 cm.

as well as in the Nujiang, Baoshan (Figs 1A, 4G), Dehong, Pu'er, and Honghe regions of Yunnan. It has not been found in Xishuangbanna, which borders Laos and has relatively low altitudes. This aligns with the opinion of Paukstadt and Paukstadt (2008): the samples from Laos identified as *A. castanea* in Brosch et al. (1999) were determined incorrectly. The giant moths of *A. castanea* are beautifully castaneous, as suggested by the etymology of its specific name. Our observations show that these adults emerge from May to August in the wilds of Tibet and Yunnan, which corresponds with the Burmese records provided by Racheli (2008), and are possibly univoltine in nature (see also Sections 3 and 4 of Results). Recently, material from the border between Vietnam and Yunnan has been correctly identified by local entomologists (e.g., Lien et al. 2014; Wu 2017: 150–151). In summary, *A. castanea* should be seen as a montane and summer-flying species endemic from northeastern India (and southeastern Tibet) to northern Myanmar, through western and southern Yunnan, extending to northwestern Vietnam but seemingly excluding Laos. Irungbam and Irungbam (2019) mentioned a Bhutanese distribution of *A. castanea* but provided no supporting specimens.

However, due to the similarity between adults and partial habitat overlap, *A. castanea* was previously misidentified as a subspecies or synonym of *A. assamensis* (e.g., Bryk 1944; Holloway 1987; d'Abrera 2012: 126–127; Kumar et al. 2016). Alternatively, specimens of the former were erroneously attributed to the latter (e.g., Seitz 1926–1928: 55B; Villiard 1969: 78; Yang et al. 2015:

533; Yi et al. 2015: 35). Furthermore, Paukstadt et al. (1998) corrected the erroneous combination "*A. castanea youngi*," which had previously been misapplied to the Thai *A. assamensis* (e.g., Nässig et al. 1996; Lampe 2010: 274), as stated by Peigler (2010).

Compared to other *Antheraeopsis* populations, several characteristics of *A. castanea* male genitalia are autapomorphic (Paukstadt et al. 1999), in addition to its uniquely pointed forewing apex (Bouvier 1936: 161). It is possible that *A. castanea* is the sister group to all other species within *Antheraeopsis*. Since past studies based on adult specimens and shorter COI sequences have not addressed this issue, dedicated research on the previously unknown preimaginals of *A. castanea* would help to clarify its phylogenetic position. Additionally, this would allow higher-quality genomes to be incorporated into phylogenetic analyses.

Materials and methods

Collection and rearing

This paper utilizes the eggs from a total of six wild-caught ♀♀ *A. castanea* for subsequent life history studies. Data for the moths are as follows: No. 1, Lüchun County, Honghe, Yunnan, 1288 m, 18 July 2023; No. 2, same location, 19 July 2023; No. 3, Jinping County, Honghe, Yunnan, 1387 m, 19 June 2024; No. 4, same location, 29 June 2024; No. 5, same location, 2 July 2024; No. 6, Mêdog County, Nyingchi, Tibet, 2182 m, 27 June 2025. Among them, the eggs of ♀♀ Nos. 1–4 and 6 were reared by Liu ZY in Wuhua District, Kunming, Yunnan (1920 m); ♀♀ Nos. 1–5 were reared by Hu CX in Mengzi, Honghe, Yunnan (1285 m); and ♀ No. 3 was reared by He MY in Anyuan District, Pingxiang, Jiangxi (112 m). The samples used for morphological description are those of Liu ZY, with the following terminology abbreviations: L1–5 = 1st–5th larval instars; T1–3 = 1st–3rd thoracic segments; A1–10 = 1st–10th abdominal segments. The dimensional data described in the Results are based on measurements of single samples (n = 1).

The general equipment used includes a vernier caliper INSIZE 1108-150C 0–150 mm/0.01 mm (± 0.02 mm) (general lengths); a thermohygrometer BENETECH GM1365 (± 2 RH%; ± 0.3 °C) (humidity and temperatures); a NIKON D5500 with a LAOWA 60 mm f/2.8–22 lens (Figs 1, 3, 4A–F, 5); and a SIGMA 10–20 mm f/4–5.6 lens (Fig. 4G). One unhatched *A. castanea* ovum (surface-dried and sputter-coated) was used for scanning electron microscope (SEM) imaging with a ZEISS GEMINISEM 360 (Fig. 2).

Molecular sequencing and phylogenetic analysis

One contribution of this study is the provision of two new complete mitochondrial genome (CMG) sequences. The tissue was ground in liquid nitrogen, followed by DNA extraction using 1 ml of preheated (65 °C) CTAB buffer with 2% β-mercaptoethanol and 50 µl of proteinase K (20 mg/ml). DNA was purified by chloroform–isoamyl alcohol (24:1) extraction, isopropanol precipitation, and RNase A treatment. Nucleic acid concentration was measured using INVITROGEN QUBIT 3.0 with the QUBIT dsDNA HS Assay Kit, and integrity was assessed by 1% agarose gel electrophoresis. For library preparation (using the VAHTS Universal Plus DNA Library Prep Kit for Illumina-ND617), we followed the ILLUMINA DNA Prep Protocol (#1000000025416), which included enzymatic fragmentation, end repair with 3′ adenylation, adapter ligation, PCR amplification, and product purification using VAZYME DNA Clean Magnetic Beads. Paired-end sequencing was carried out on an ILLUMINA NOVASEQ 6000 platform using libraries that passed quality control. The samples used are as follows:

- *Antheraea castanea*: An L_1 larva from ♀ No. 3 (see above), hatched from ovum on 2 July 2024. It was killed on 5 July 2024 and preserved in 95% (± 5%) ethanol at −18 °C until 13 January 2025 for sequencing.
- *Antheraea youngi*: A ♂ adult from Trus Madi Entomology Camp, Keningau, Sabah, Malaysia, 1183 m, captured and killed on 6 February 2023, then stored dry in a triangular envelope at room temperature. Thoracic muscles were extracted for sequencing on 13 January 2025.

The CMG assemblies were performed using SPADES 3.15.4 (Prjibelski et al. 2020), then annotated with MITOS2 (Donath et al. 2019) and manually curated for accuracy. The corresponding high-throughput files are accessible in NCBI BioProject PRJNA905660. OGDRAW (Greiner et al. 2019) was used to draw the linear map, followed by manual visual optimization with AFFINITY PHOTO 2 (Fig. 6).

We followed the suggestion of Liu (2024) to use CMGs rather than the 13 protein-coding genes (PCGs) to construct the first phylogenetic tree (Suppl. material 1: tree S1). In addition to our new sequences, this dataset includes 39 other species of Saturniidae, with two taxa from Bombycidae and one from Lasiocampidae selected as outgroups (Suppl. material 1: table S1). Sequence alignment was performed using MAFFT 7 (Katoh et al. 2019) with default settings, and phylogenetic inference was conducted using IQ-TREE 2 (Minh et al. 2020) under the best-fit model GTR + F + I + R5, chosen according to BIC (Kalyaanamoorthy et al. 2017), with ultrafast bootstrap (1,000 replications) (Hoang et al. 2018).

For the second tree (Suppl. material 1: tree S2), we selected COI barcodes for 10 *Antheraeopsis* spp. (based on the complete list of 12 species provided by Kitching et al. 2018, excluding the uncertain *A. inthanonensis* and *A. tenasserimensis*). Three to five sequences for each species (from or close to the type locality) were downloaded from BOLD Systems 4 (v4.boldsystems.org) (Suppl. material 1: table S2) and added to the above CMG dataset. The alignment and tree generation were performed using the same software and parameters. The resulting complete topologies of the two maximum likelihood (ML) trees were preliminarily visualized with ITOL 6 (Letunic and Bork 2021), followed by manual color and layout design using AFFINITY PHOTO 2 (Fig. 7).

To improve clarity, we created an approximate current distribution map for *Antheraeopsis* spp. (Fig. 7). It is primarily based on logical inferences from our phylogenetic analysis, supplemented by specimens from China, Vietnam, and Borneo in our collection. Additionally, records from all available literature listed in the References were consulted, with preference given to those from dedicated taxonomic studies (e.g., Brechlin 2001; Paukstadt and Paukstadt 2008). In this work, we do not comment on the taxonomic handling of other *Antheraeopsis* taxa by Kitching et al. (2018) aside from *A. castanea*.

Results

1. Immature stages of *A. castanea* from southeastern Yunnan (based on offspring of ♀ No. 3)

1.1. Ovum (Figs 2, 3A): The overall shape is tri-axial ellipsoid (2.65*2.22*1.68 mm), with a grayish chorion covered by dark brown glue. The micropylar rosette is composed of polygonal imprints left by follicle cells. Crowned aeropyles are dispersed across the external surface, except in and immediately around the micropylar zone.

1.2. L_1 (Fig. 3B, C): The shiny red-brown head capsule is 1.28 mm wide, with long white bristles anteriorly. The cervacoria is gray. The ground color from T_1 to A_{10} is yellow, vivid dorsally and pale ventrally. Each of T_2–A_8 has two black transverse stripes, one anterior and one posterior, to the segmental transverse row of subdorsal and dorsal scoli. Additionally, a black stripe decorates each segmental junction from T_1 to A_8. The dorsal midline T_2–A_8 is dark in color. The prothoracic shield is black, with forward-pointing and curved primary setae at the anteromarginal position (borne on the tactile dorsal and subdorsal scoli). Most other scolus bases are the same yellowish color as the surrounding integument; they bear gray, slightly curved primary setae. However, the lateral and subdorsal scoli of T_1–A_1, the subdorsal scoli of A_9, and the dorsal scoli of A_{10} show more melanin at their bases and hairs, with the melanin extending into the surrounding areas. A pair of dorsal scoli are fused medially on A_8. The sclerites of the legs $T_{1–3}$ are smooth and dark brown, while the prolegs $A_{3–6}$ are pale yellow, the same color as the venter. The lateral plate of proleg A_{10} and the postcentral area of the anal shield are black.

1.3. L_2 (Fig. 3D, E): The width of the head capsule is 2.12 mm, and its color is the same as in L_1, but the cervacoria has changed to light ochre. The integument is generally yellowish-green, and the black transverse stripes present in the previous instar are now absent. The dorsal midline from T_2 to A_8 is dark green. In the lateral view, the subdorsal scoli of $A_{1–9}$ are connected by a horizontal olive-green stripe. In some individuals, a similar but very faint stripe connects the dorsal scoli from T_2 to A_8, though it is absent in others. The black prothoracic shield is divided by a light yellow midline. All primary setae of non-(sub)ventral scoli are black, with the longest ones appearing on the tactile dorsal and subdorsal scoli of T_1. Additionally, all lateral, subdorsal, and dorsal scoli have a bluish-purple base. The lateroproximal area of each dorsal scolus from T_2 to A_9 displays a metallic silvery zone, though it has not fully developed yet. All spiracles are brown in color but paler on A_8. The brown legs of $T_{1–3}$ are lighter than in L_1, and a subcircular black spot has developed on each proleg $A_{3–6}$. The plantar lateral surfaces are light brown. For the late period, its greenish hue from T_1 to A_{10} becomes more pronounced. The bluish-purple warts appear more vivid, with enhanced metallic silver zones. A supraspiracular yellow band begins to develop, extending from A_1 to A_{10}. Each segment from A_2 to A_7 is adorned with an oblique dark green subspiracular stripe.

1.4. L_3 (Fig. 3F, G): The head capsule measures 3.69 mm in width, with coloration similar to L_2. The previously distinct dark dorsal midline observed during $L_{1–2}$ has nearly disappeared. The supraspiracular yellow band present in L_2 becomes more conspicuous, while most other integumentary areas transition to green. All non-(sub)ventral scolus bases turn pinkish-purple except for the persistently blue dorsal scoli of A_{10}. The dorsal silvery spots become more lustrous. The proximal areas of the coxae $T_{1–3}$ and the lateral integument of T_1 exhibit brighter yellowish tones. Several black dots develop on the lateral areas of prolegs $A_{3–6}$, each bearing a seta. The lateral plate of proleg A_{10} appears subtriangular, yellow superiorly and black inferiorly, surrounded by a light brown fleshy "ring". The postcentral black patch on the anal shield shrinks into a "V-shape", flanked by brown fleshy margins. A transverse row of yellow hairs appearing on the anterior region of each $A_{1–8}$. Short and crossed white setae emerge at the dorsal junctions of A2/A3, A3/A4, A4/A5, A5/A6, and A6/A7. All spiracles except the white one on A_8 turn black, and their inferior oblique stripes (visible only on $A_{2–7}$) become more distinct compared to L_2.

1.5. L_4 (Fig. 3H): Despite little change in coloration from the previous instar, the head capsule width increased to 5.23 mm. The cervacoria is pale wine-colored. The paired black spots on the prothoracic shield during $L_{2–3}$ completely disappear, replaced by bright yellow-green pigmentation that intensifies along the anterior margin of T_1 and on the coxae $T_{1–3}$. The supraspiracular yellow band becomes strikingly vivid, edged with light brown from A_3 to A_9 (increasingly prominent posteriorly, but not visible on $A_{3–6}$ in some individuals). The subspiracular oblique stripes present in $L_{2–3}$ are very inconspicuous or even disappear. All lateral, subdorsal, and dorsal scoli develop mulberry-colored bases except those on T_1, which appear light ochre. The short and crossed white setae

observed in L_3 now additionally appear at the A1/A2 junction, while the transverse yellow setal rows on the anterior zones of $A_{1–8}$ become more developed, with clubbed tips. The pattern on A_{10} resembles that of L_4, but the lateral plate turns completely green, with a darker peripheral "ring". The "V-shaped" postcentral black spot on the anal shield splits centrally into two parts, fading from black to brown, with its central area replaced by bright green.

1.6. L_5 (Fig. 3I–R): This is the mature instar, with a head capsule 7.57 mm wide. The overall coloration of the head capsule is pale brownish-red, with dark brown processes on the lateral areas. While superficially similar to L_4, several distinct morphological changes are evident. The overall green integument has become lighter in the dorsal area while simultaneously darkening ventrally, resulting in a more pronounced countershading effect. All scoli that possessed a mulberry-colored base in the previous instar have now shifted to a vivid purple. Furthermore, the warts T_1, previously light ochre during L_4, are now a distinct lemon-yellow, and this yellow pigmentation is intensified across the entire anterior region of this segment—including the coxae but excluding the cervacoria—giving it a brighter and more vivid appearance. Notably, the majority of the yellow setae located on the anterior zones of $A_{1–8}$, which were described in L_4 as "having clubbed tips," have now reverted to pointed tips.

1.7. Pupa (Fig. 4B–F): The pupal case is dark brown, except for a translucent 'window' between the compound eyes. The medial margins of the antennae do not meet along the ventral midline, and both the maxillae and the legs $T_{1–2}$ are visible. Spiracle T_1 appears as a narrow gap at the boundary between T_1/T_2; the spiracles $A_{2–7}$ are well developed, but the spiracle A_8 is likely a remnant. A pair of forewing tubercles is located on the dorsolateral regions of T_2. The male genital pore appears as a navel-like scar on the midventral A_9. The terminal A_{10} bears pointed cremaster hooks.

1.8. Cocoon (Fig. 4A): The freshly spun cocoons appear white in a relatively dry environment (ca. 50–70% RH), but after full oxidation (100% RH, 48 h), they turn light brown. The upper terminal end of the cocoon features a peduncle that wraps around the host plant, with the pupal head oriented upward and the exit side completely sealed. Cocoons are enclosed by surrounding leaves for protection.

2. Immature stages of *A. castanea* from southeastern Tibet (based on offspring of ♀ No. 6)

Although SEM observation was not conducted, the external morphology, size, and coloration of the eggs are nearly identical to those of the specimens from Yunnan (see also Section 1.1). The $L_{1–3}$ caterpillars are also generally consistent with the descriptions provided in Sections 1.2–1.4. However, several notable differences were observed: in the Tibetan population, all bluish-purple scolus bases—which are present in Yunnan L_2 larvae—are bright aquamarine. Except on T_1, these warts exhibit a distinctive yellow upper portion and a pinkish lower portion throughout $L_{3–5}$. Another conspicuous distinction is the presence of more or less shiny, clubbed setae on all major scoli in $L_{4–5}$ (Fig. 5A, B), a feature not observed in Yunnan larvae. Furthermore, the dorsal yellow hairs with clubbed tips, which were documented in Yunnan L_4 larvae, are consistently present in both L_4 and L_5 of the Tibetan lineage.

The larvae from Yunnan exhibit a darker appearance in the head capsule and legs $T_{1–3}$ during $L_{2–5}$ compared to those from Tibet. Furthermore, the brownish areas on A_{10} in $L_{4–5}$ are also darker in the Yunnan population than in the Tibetan one (Fig. 5C, D) (see also Sections 1.5 and 1.6). The pupae and cocoons both conform to the descriptions provided in Sections 1.7 and 1.8.

3. Rearing report of *A. castanea* from southeastern Yunnan (based on offspring of ♀ No. 3)

During the summer rearing of 2023, all L_1 larvae of Liu ZY perished within one week after feeding on *Camphora officinarum* (Lauraceae) and *Cinnamomum burmannii* (Lauraceae). In contrast, Hu CX successfully reared a few individuals to L_2 using the latter plant but did not continue observations. In the summer of 2024, the three authors re-evaluated these two plants, and all tested larvae once again died during L_1.

Liu ZY subsequently offered *Quercus yunnanensis* (Fagaceae), *Alnus nepalensis* (Betulaceae), and *Liquidambar formosana* (Altingiaceae) to 21 newly hatched L_1 individuals, all of which completely rejected these

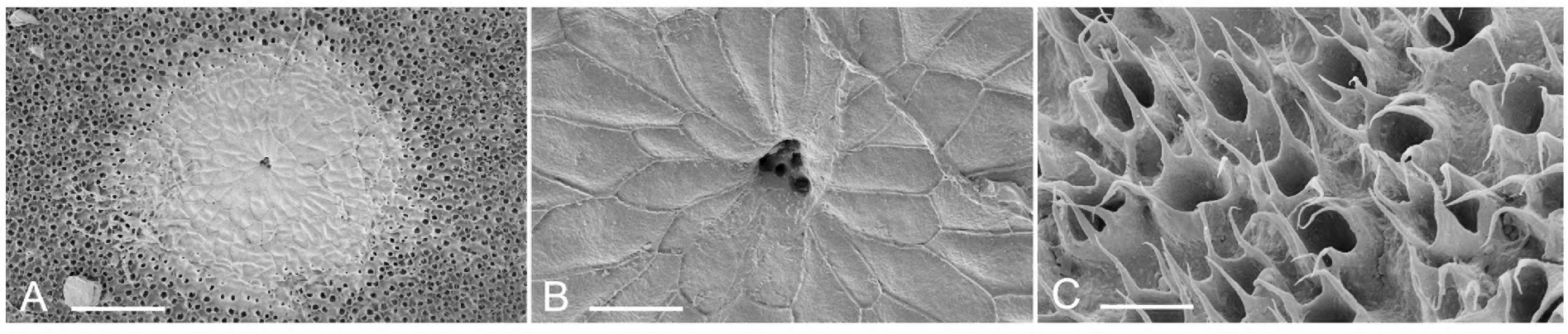

Figure 2. Chorion of *Antheraea castanea*, SEM. **A.** The anterior pole, whose central area is the micropylar zone; **B.** Micropylar rosette; **C.** Aeropyle crowns. Scale bars: 100 μm (**A**); 20 μm (**B**); 10 μm (**C**).

Figure 3. Ova and $L_{1–5}$ of *Antheraea castanea* from southeastern Yunnan. **A.** Ova; **B, C, E.** On host plant *Litsea populifolia*; **D, F–R, R.** On host plant *Camphora septentrionale*; **B.** L_1, lateral view; **C.** L_1, dorsal view; **D.** L_2, lateral view; **E.** L_2, dorsal view; **F.** L_3, lateral view; **G.** L_3, head and $T_{1–3}$, anterolateral view; **H.** L_4, lateral view; **I.** L_5, lateral view; **J.** L_5, dorsal view; **K.** L_5, subdorsal scolus of A_2, apicolateral view; **L.** L_5, dorsal scolus of A_2, apicolateral view; **M.** L_5, dorsal scoli of A_8 (medially fused), apical view; **N.** L_5, leg T_3, lateral view; **O.** L_5, head and $T_{1–2}$, anterolateral view; **P.** L_5, A_{10}, dorsal view; **Q.** L_5, A_{10}, lateral view; **R.** L_5, spinning the external part [floss] of cocoon, dorsal view. Scale bars: 1 mm (**K**); 2 mm (**L, M**); 3 mm (**A, N**); 1 cm (**D, E**); 5 mm (**B, C, G, O–Q**); 1.5 cm (**F, H, I, J, R**).

Figure 4. Cocoon and pupa of *Antheraea castanea* from southeastern Yunnan. **A.** Cocoon, spun and stored in a dry environment, lateral view; a: peduncle; b: the exit side; **B–F.** Pupa ♂; **B.** a: lateral view; b: ventral view; c: dorsal view; **C.** Head and $T_{1–2}$, ventrolateral view; **D.** $T_{1–2}$, dorsolateral view; a: spiracle T_1; b: forewing tubercle; **E.** ventral view; a–c: $A_{8–10}$ (the genital pore is located at the center of A_9); **F.** Cremaster on the tip of A_{10}, dorsal view; **G.** The habitat in Gaoligong Mountains, Baoshan, Yunnan Province, China, 2214 m, 24 ♂♂ were collected here on 21 June 2024 and 21–23 June 2025 by Liu ZY. Scale bars: 1 mm (**F**); 1.5 mm (**E**); 3 mm (**C. D**); 8 mm (**B**); 1 cm (**A**).

options. Ultimately, after accepting *Litsea populifolia* (Lauraceae) and *Camphora septentrionale* (Lauraceae) (rearing under conditions of 16.5–25.8 °C with ca. 70.6–90.4% RH), nine individuals successfully spun cocoons. However, three of these died during the pre-pupation, while the remaining six pupae are all male.

L_1 caterpillars live independently on the undersides of leaves without integumentary contact with others, though 2–4 individuals may occasionally be found on the same leaf. When at rest, they typically assume a "J"-shaped posture. During $L_{2–5}$, larvae are still generally solitary, residing either on the undersides of leaves or at the branches. As with most saturniids, supplementary water is essential for larval development. The larvae of $L_{4–5}$ usually detach their legs $T_{1–3}$ (sometimes including prolegs $A_{3–4}$) from the vegetation, and during $L_{2–5}$ they were consistently observed orienting their heads toward the side with higher illuminance. After feeding ended [liquid defecation], larvae all spun cocoons on host plants. The scoli of the whole larval stage have no visible exocrine secretion, without irritation to human skin. When the mature larvae are attacked, they will

Figure 5. Mature larvae of *Antheraea castanea* from southeastern Tibet, on host plant *Litsea rubescens*. **A.** L_5, lateral view; **B.** L_5, dorsal scolus of A_4, lateral view; **C.** L_5, head and $T_{1–3}$, anterolateral view; **D.** L_5, A_{10}, dorsolateral view; Scale bars: 2 mm (**B**); 5 mm (**C, D**); 1.5 cm (**A**).

shake T_1–A_3 from side to side, sometimes clicking the mouthparts to make noise.

The developmental calendar is as follows (1 ♂, fed on *C. septentrionale* in 2024): 20 June, oviposited; 01 July, hatched into L_1; 06 July, 1st pre-ecdysis; 07 July, molted into L_2; 12 July, 2nd pre-ecdysis; 13 July, molted into L_3; 17 July, 3rd pre-ecdysis; 18 July, molted into L_4; 25 July, 4th pre-ecdysis; 27 July, molted into L_5; 12 August, feeding ended and spun cocoon. On 28 May 2025, the moth emerged from its cocoon.

4. Rearing report of *A. castanea* from southeastern Tibet (based on offspring of ♀ No. 6)

Based on the rearing experience in 2023–2024 (see also Section 3), during the summer of 2025, a total of 99 L_1 larvae (from 137 eggs) were reared on *C. septentrionale* and *Litsea rubescens* (the only available *L. populifolia* had died and was therefore unusable), under conditions of 17.8–26.4 °C with ca. 66.3–87.4% RH. The latter host was more readily accepted by newly hatched caterpillars than the former. Compared with the L_1 group reared on *L. rubescens*, those provided with *C. septentrionale* exhibited higher mortality and slower developmental progression, invariably failing to reach the L_2. Therefore, all surviving larvae were ultimately reared on *L. rubescens*. Ultimately, seven mature larvae spun cocoons directly on this host plant, whereas the remainder left the vegetation, yielding a total of 35 cocoons. The period from initial oviposition to the spinning of the last cocoon extended from 27 June to 24 August. As of 19 September, no adult emergence had been recorded. Other biological traits observed during the larval stage were consistent with the corresponding descriptions provided in Section 3.

5. Phylogenetic Analysis on *A. castanea* and *Antheraeopsis*

The CMG sequence lengths are 15,325 bp for *A. castanea* (GenBank accession number: PV136007) and 15,307 bp for *A. youngi* (GenBank accession number: PV136008) (Fig. 6).

In the CMG-based phylogeny, all *Antheraeopsis* nodes received maximal support, whereas certain nodes in the CMG + COI topology showed lower support (Fig. 7). The two results form a single topology, indicating that the subgenus *Antheraeopsis* is composed of three major species groups. The CMG + COI tree shows a monophyletic group of four species [((*A. assamensis* + *A. rudloffi*) + *A. chengtuana*) + *A. formosana*] is distributed across the mainland of Southeast Asia and its northern tropical and subtropical territories (the "cool colors" in Fig. 7), i.e., the *assamensis*-group. Meanwhile, another lineage occupies Sundaland and the Philippines (the "warm colors" in Fig. 7), known as

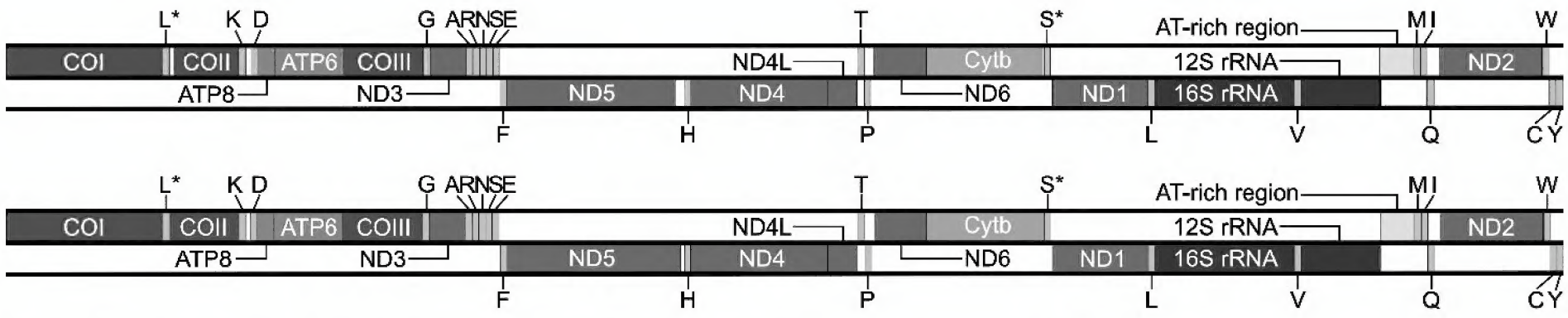
L* K D G ARNSE T S* AT-rich region M I W
COI COII ATP6 COIII ND4L Cytb 12S rRNA ND2
ATP8 ND3 ND5 ND4 ND6 ND1 16S rRNA
F H P L V Q C Y
L* K D G ARNSE T S* AT-rich region M I W
COI COII ATP6 COIII ND4L Cytb 12S rRNA ND2
ATP8 ND3 ND5 ND4 ND6 ND1 16S rRNA
F H P L V Q C Y

Figure 6. Linear map of the CMGs of *Antheraea castanea* (top) and *Antheraea youngi* (bottom).

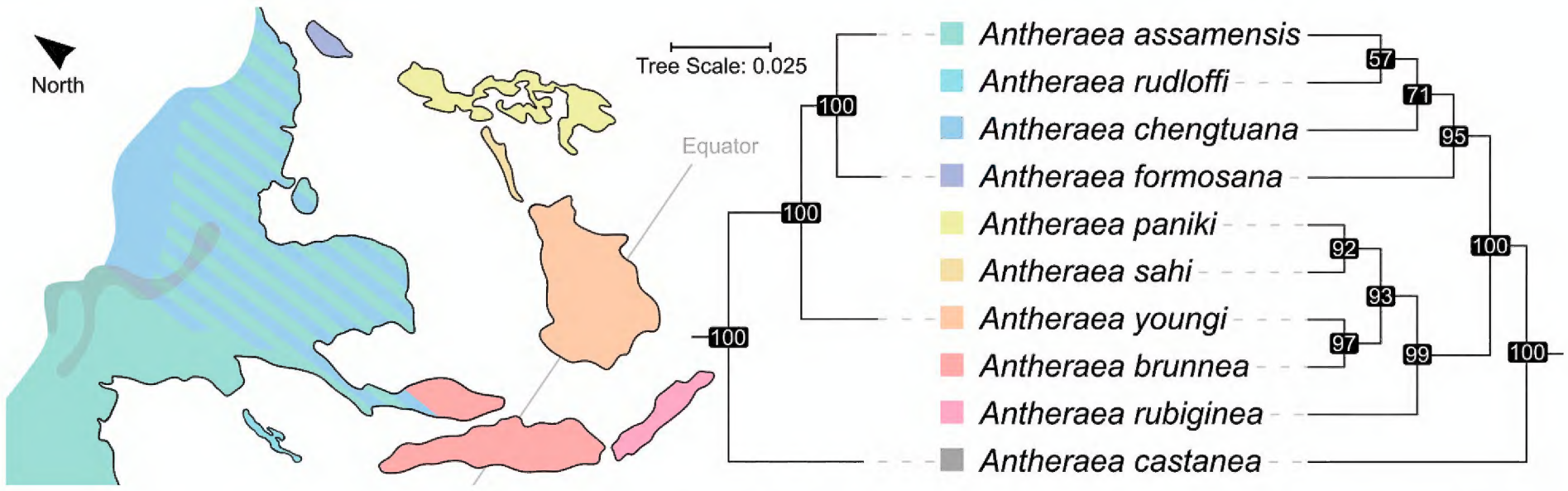

Figure 7. Intrasubgeneric phylogeny of the subgenus *Antheraeopsis* and current distribution. The stripes on the map (at the leftmost) indicate "uncertain ranges." The phylogenetic tree on the left is the CMG result (Suppl. material 1: tree S1), and the one on the right is based on CMG + COI (Suppl. material 1: tree S2); the tree scale is only for the CMG result. The colors of the map correspond to the colors of the taxa on the phylogenetic trees.

the *youngi*-group, which contains five species [((*A. paniki* + *A. sahi*) + (*A. youngi* + *A. brunnea*)) + *A. rubiginea*]. *A. castanea* is the sister taxon to these two clades.

Discussion

Although the caterpillars from Honghe, Yunnan, and Mêdog, Tibet, exhibit some morphological differences, we currently do not propose to treat them as separate species—specifically, we refrain from resurrecting the name *A. mezops* for the former population or naming the latter as a new species. This decision is based on several factors: no life-history data are available from Meghalaya, western Yunnan, or northern Myanmar, and the genitalia of the Tibetan moths require further study, as no males have yet been obtained from field collection or rearing experiments. Moreover, even if the two were to be classified as distinct subspecies or species, they would still represent the closest known sister lineages within the subgenus *Antheraeopsis*, and these differences are not supported by reliable diagnostic characters in the imaginal external morphology, at least in females. Technically, any potential future taxonomic revisions would not affect the current discussion, which treats material from Yunnan and Tibet as a monophyletic group under the name *A. castanea*.

Regier et al. (2005) described the eggshell of *A. rubiginea* (originally as "*A. youngi* from Java," then corrected by Paukstadt and Paukstadt (2010)) as "the aeropyle crowns were uniformly distributed across the eggshell except immediately surrounding the region of the micropyle at the anterior pole." Kumar and Kamble (2008) stated that "all the aeropyles of *A. assamensis* were covered with a cup-shaped structure, and the terminals of this structure have many finger-like projections." Our observations on *A. castanea* confirm that its aeropyle crown distribution pattern aligns with those of the two aforementioned species.

Indian authors have published many morphological studies on the life history of *A. assamensis* (e.g., Jolly et al. 1979: 122–126; Goswami and Singh 2012; Kakati et al. 2012), while Lampe (2010: 274) and Wu (2017: 135–144) have illustrated the immature stages of the Thai and Chinese populations, respectively. Recently, Veenakumari et al. (2011) found some wild larvae of *A. rudloffi* from the southern Andaman. We have reared materials from Yunnan and Hainan, which we temporarily refer to as *A. assamensis*, as their larvae appear nearly indistinguishable from the caterpillars of *A. chengtuana* from Ya'an, Sichuan, and *A. assamensis* from Mêdog, Tibet (reared by Liu ZY in 2022 and 2025, respectively). The preimaginal *A. formosana* from Taiwan are also documented in several works (e.g., Lin et al. 1993; Wang 1994: 51–57; Wang and Heppner 1994; Peigler and Wang 1996: 240–245). Paukstadt and Paukstadt (2001) provided a complete life cycle of the Javanese *A. rubiginea* (originally as "*A. youngi*," corrected by Paukstadt and Paukstadt (2010)). Additionally, van Eecke (1929) figured a mature larva of *A. brunnea* from Sumatra and provided a brief description. In all the compared specimens, L_1 consistently exhibited a shiny black or blackish-brown head capsule, yellow dorsal coloration with black transverse stripes on T_1, and a lateral black spot at the base of each proleg on $A_{3–6}$. Despite variations in dorsal scolus coloration (ranging from black to light gray), these larvae are macroscopically indistinguishable. In comparison, *A. castanea* has a red-brown head capsule with an almost entirely black dorsum T_1 and no black markings on the prolegs $A_{3–6}$. Moreover, in $L_{2–3}$ of *Antheraeopsis*, as known in the past, a continuous dark green stripe runs along each side (divided along the dorsal and ventral midlines), connecting the dorsal scoli from T_2 to A_8. Nässig (1991) identified this as a subgeneric synapomorphy; however, in *A. castanea*, it appears indistinct. For $L_{4–5}$, morphological features that could identify specific populations are no longer discernible except for *A. castanea* from Tibet, which has characteristic clubbed setae. However, we currently know that the "yellow-green lateral plate of proleg A_{10} is ringed by a black or dark brown zone (mature larva)" is exhibited by all members of *Antheraeopsis*—it may actually function as an eyespot playing a role in defensive warning. This feature is not present in any other known *Antheraea*

larvae (subgenera *Antheraea* and *Telea* Hübner, 1819). Näs-sig et al. (1996) accurately diagnosed this characteristic.

Muga reeling silk is typically golden, but cocoon coloration varies from white to brown among populations, and the degree of calcium oxalate crystal deposition also differs (Kalita and Dutta 2020). In relatively dry indoor environments, *A. castanea* cocoons are white, but they oxidize to a light brown color when thoroughly wet. Unfortunately, we currently lack valid data (analysis based on silk protein components or microstructures) for comparing the cocoons between *Antheraeopsis* spp.—similar to their pupae, distinguishing them based solely on external appearance is difficult.

Host plant tests for *A. castanea* confirm a strong oligophagous tendency, with larvae feeding exclusively on select species within the family Lauraceae. Larvae from Tibet exhibit a higher degree of host specialization compared with those from Yunnan. Based on current limited experiments, they can complete development exclusively on *Litsea* but fail to feed on *Camphora*. In contrast, the Yunnan population utilizes both genera as hosts, although only certain species within *Camphora* are acceptable. The well-known natural foods of *A. assamensis* include *Machilus gamblei* and *Litsea monopetala* (e.g., Seidel and Peigler 2018; Selk 2023: 146), as well as the normal hosts of *A. formosana*, *A. rudloffi*, and *A. brunnea*, such as *Camphora*, *Persea*, *Lindera*, *Litsea*, and *Cinnamomum* (all Lauraceae) (van Eecke 1929; Wang 1994: 51–57; Veenakumari et al. 2011). Despite sporadic reports of *A. assamensis* feeding on oaks (e.g., Crotch 1956: 55; Arora and Gupta 1979; Robinson et al. 2001: 48; Meister 2011: 148) and more botanical families listed by Devi et al. (2021), Paukstadt and Paukstadt (2001) used Himalayan birch (Betulaceae) to feed *A. rubiginea*. Our experiences—besides those of Baxter (1992: 29) and Nässig et al. (1996)—indicate that any non-lauraceous plants were poorly accepted under laboratory conditions. Furthermore, due to the lack of detailed descriptions, we are uncertain whether *Fagus sylvatica* (Fagaceae) and *Laurus nobilis* (Lauraceae) listed by Meister (2011: 148) for "*A. castanea*" are correct, as they likely stem from saturniid misidentification—the former plant was provided by Lampe (2010: 358) for "*A. castanea youngi*" (actually *A. assamensis*; see Introduction).

Nässig and Treadaway (1998) suggested that *Antheraeopsis* caterpillars are oligophagous lauraceous feeders, and in light of the new data on *A. castanea*, we further confirm this. In contrast, the other two subgenera are not associated with Lauraceae (Nässig et al. 1996), but *Quercus* (Fagaceae) is widely shared in their diets (e.g., Paukstadt et al. 2003: table 4), and they even specialize in it (e.g., Liu 2023), especially in the "basal/relict clades," the pernyi group (for subgenus *Antheraea*) and the compta group (for subgenus *Telea*) (sensu the NJ barcode tree in Peigler and Naumann 2016, though further clarification is needed). Liu (2024) speculated that oaks are the most original host plants of the genus *Antheraea*.

Paukstadt and Paukstadt (1998) considered the subgenus *Antheraeopsis* to consist of the *assamensis*- and *youngi*-groups, and regarded *A. castanea* as belonging to the former. Following the system of Paukstadt et al. (2000), *A. assamensis* + *A. castanea* form the sister group to intrasubgeneric *A. chengtuana*, *A. formosana*, *A. brunnea*, *A. youngi*, *A. rubiginea*, *A. sahi*, and *A. paniki*. Brechlin (2002) and Paukstadt and Paukstadt (2008) suggested that *A. rudloffi* belongs to the last lineage. In the most recent versions of Paukstadt and Paukstadt (2013a, 2013b, 2020, 2022, 2023a, 2023b, 2024a, 2024b), these silkmoths were classified into five groups: (1) *A. assamensis* (*A. inthanonensis* and *A. tenasserimensis* included) + *A. rudloffi*, (2) *A. castanea*, (3) *A. chengtuana* + *A. formosana*, (4) *A. brunnea* + *A. youngi* + *A. rubiginea* + *A. sahi*, and (5) *A. paniki*—although the accurate phylogeny was not mentioned.

The complete topologies of our ML trees (Suppl. material 1: trees S1, S2) align fully with Liu (2024) at the subfamily and tribal levels. Notably, the subfamily Saturniinae (*Antheraeopsis* included) was resolved as (Saturniini + Attacini) + Solini, which has previously been corroborated by Rougerie et al. (preprint). The molecular results strongly support that the subgenus *Antheraeopsis* consists of three basic species groups: (1) *assamensis*-group (four species); (2) *youngi*-group (five species); and (3) *castanea*-group (one species). The latter is the sister of the first two. However, due to the current availability of only incomplete COI sequences for multiple species, this work does not attempt to resolve the precise phylogeny within groups. Future higher-quality genomic or more detailed morphological studies will help clarify such finer details. For example:

1. Differentiation within the *assamensis*-group needs to be further confirmed, as it may contain subjective synonym relationships. Wu (2017: 139–144) specified partial material from Yunnan and Guangdong as *A. formosana*, but for the latter province, Morishita and Kishida (2000), Li et al. (2011), and Wang et al. (2020: 164–165) referred to related specimens as *A. assamensis*. Cheng et al. (2023) identified the samples from Zhejiang as *A. assamensis*, while the moths from Vietnam and Laos have been labeled *A. chengtuana* and *A. assamensis*, respectively (Pham et al. 2019; Kishida et al. 2020).
2. Although Nässig and Treadaway (1998) conservatively established *A. sahi* from Palawan as a subspecies of Philippine *A. paniki*, Paukstadt et al. (1999) suggested that the former is actually closer to Bornean *A. youngi*, which is consistent with the topology "(*A. sahi* + *A. youngi*) + *A. paniki*" in the barcode tree of Paukstadt and Paukstadt (2013a). Zoogeographically, several saturniid species from Palawan and Borneo have been considered not distinct at the species or subspecies level (Paukstadt and Paukstadt 2008).

Conclusion

Whether based on CMG or COI barcode phylogeny or larval morphological comparisons, *A. castanea* is unequivocally the sister group to all other species

(*assamensis*-group + *youngi*-group) within its subgenus *Antheraeopsis*, consistent with the unique findings of Paukstadt et al. (1999) regarding its male genitalia.

Rougerie et al. (preprint: table S4) estimated that *A. castanea* and its sister group diverged approximately four million years ago. Given the current distribution of the crown group, it is reasonable to infer that this speciation occurred in the subtropical forests at the eastern end of the Himalayas (near the present range of *A. castanea*), which suggests the subgeneric origin. Interestingly, *Telea* may have a similar evolutionary history—most species of this subgenus are distributed in the New World, with only one sub-Himalayan taxon, the relict *Antheraea compta* Rothschild, 1899 (e.g., Peigler 1999), which shares a nearly identical habitat with *A. castanea*, though the former has been found to be oligophagous on oaks (Liu 2023). Within the genus *Antheraea*, the precise feeding preference for Lauraceae is an autapomorphy of the subgenus *Antheraeopsis*, and we propose that this lineage diverged from its oak-feeding and later polyphagous ancestors through host plant exploration and selection, accompanied by an increasing dependence on the laurel family.

We propose referring to *A. castanea* as "pseudomuga" (pseudo-, false) to help Asian entomologists distinguish it from the "true" muga *A. assamensis* and to encourage greater attention to the former in future field sampling and breeding efforts.

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Supplementary material 1

Original forms of the mtDNA trees, with the used sequences

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